Long-term interval burning alters fine root and mycorrhizal dynamics in a ponderosa pine forest

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Summary

1. Plant roots and their mycorrhizal symbionts are critical components of forest ecosystems, being largely responsible for soil resource acquisition by plants and the maintenance of soil structure, as well as influencing soil nutrient cycling. Silvicultural treatments should be guided by knowledge of how these below-ground components respond to different forest management practices.

2. We examined the cumulative effects of 20 years of prescribed burning at 2-year intervals. We measured fine root length density and fine root and mycorrhizal root biomass in the upper 15 cm of mineral soil in a south-western ponderosa pine forest over a complete burn cycle.

3. Repeated burning reduced fine root length, fine root biomass and mycorrhizal root biomass, as well as the amount of nitrogen and phosphorus stored in these below-ground pools.

4. Estimates of fine root production, fine root decomposition and nutrient dynamics were similar in burned and control plots.

5. *Synthesis and applications.* Although repeated-prescribed fire may be an effective, low-cost approach for reducing fuel loads and lessening the chance of a catastrophic wildfire in ponderosa pine forests, our results suggest that this strategy may negatively affect below-ground biomass pools and nutrient cycling processes in the long term. We recommend that mechanical reductions in fuel loads be conducted in these and similar forests that have not experienced fire for decades, before fire is reintroduced as a management tool.

Key-words: Arizona, ecological restoration, ectomycorrhizae, fine roots, prescribed fire

Introduction

Fire has been an important part of the evolutionary history of many forests in western North America (Covington *et al*. 1994). This is especially true for ponderosa pine *Pinus ponderosa* Dougl. ex Laws.-dominated forests of the south-western USA, where fire frequency was among the highest historically of any forest type (Covington *et al*. 1994). The natural fire regime of ponderosa pine forests is characterized by frequent (every 2–20 years) low-intensity surface fires. This fire regime maintained a savanna-like vegetation structure, with small groupings of large trees within a matrix of herbaceous understorey dominated by grasses (Cooper 1960). Following Euro-American settlement in the 1880s, heavy livestock grazing, intensive logging of old-growth trees, a favourable climate and active fire suppression reduced the herbaceous understorey and allowed exceptionally high pine seedling establishment within the grass openings. Contemporary forests are often characterized as closed-canopy forests with high stand densities of small-diameter trees, deep deposits of dead organic material on the soil surface and little herbaceous understorey production. These structural changes and continued active fire suppression have also changed the fire regime to infrequent and stand-replacing (Covington *et al*. 1997). Although there have been numerous studies documenting these

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changes in above-ground forest structure since Euro-American settlement, few studies have assessed the functional changes (e.g. productivity, nutrient cycling processes and water balance) in these ecosystems that have occurred in the absence of a historical fire regime (but see Wright & Hart 1997; Kaye & Hart 1998a,b; Kaye *et al.* in press).

Increasingly, forest managers have used prescribed fire in these ecosystems to reduce fuel loadings and associated risks of wildfire, reduce tree densities and improve understorey production (Covington *et al.* 1997; Allen *et al.* 2002; Kaye *et al.* in press). Although we have considerable information on the physical and chemical changes that occur in soil following the reintroduction of fire into these ecosystems after decades without fire, we know comparatively little about the impacts of fire on the soil biota. Furthermore, few data are available on the long-term effects of fire on any ecosystem component or process over multiple fire cycles (Binkley *et al.* 1992; Wright & Hart 1997; Tuininga & Dighton 2004; Hart *et al.* in press). Frequent fire is essential in these ecosystems in order to maintain the open-canopy structure (Covington *et al.* 2001).

We took advantage of one of the few long-term replicated-interval burning studies to examine the effects of repeated-prescribed fire on fine root and mycorrhizal root biomass and nutrient dynamics over an entire burn cycle in a ponderosa pine forest of the south-western USA. The historical fire-return frequency was 2–5 years in this area (Dieterich 1980) but fire had been absent from this forest for 100 years prior to the initiation of the replicated-interval burning study in 1976 (Sackett 1980). Experimental evaluation of the long-term (decadal) impacts of repeated fires on key ecological components and functions, such as those described in our study, is vital for understanding how prescribed fire can be utilized most effectively in the restoration of these forests to conditions that existed prior to Euro-American settlement of the western USA. More generally, such experiments using fire as a management tool are prime examples of how applied ecological principles can be used to enhance ecosystem health (Russell-Smith *et al.* 1998; Freckleton 2004; Fuhlendorf & Engle 2004; Emery & Gross 2005).

Materials and methods

STUDY AREA

This study was conducted in the Chimney Spring area of the Fort Valley Experimental Forest, Coconino National Forest (111°45′W, 35°16′N), USA. The altitude ranges from 2240 to 2286 m.a.s.l. Mean annual precipitation measured 15 km from Chimney Spring is approximately 552 mm (years 1951–2000; WRCC 2000), and consists of heavy monsoonal rains in mid- to late summer and scattered rain and snowfall throughout the winter months. However, precipitation varies greatly from year to year and prolonged

droughts are common. Our research was conducted during a year with the highest precipitation over the past 50 years (1993, 1001 mm, October 1992–September 1993) and a year with near-average precipitation (1994, 636 mm, October 1993–September 1994; WRCC 2000). The average frost-free growing season is 94 days, with mean daily air temperatures ranging from −5 to 17 °C (Sackett 1980).

The interval burning study consisted of 27 contiguous 1-ha plots that had been burned at 1-, 2-, 4-, 6-, 8- and 10-year intervals (three replicates of six treatments) since 1976; the remaining nine plots were unburned areas that served as controls. All treatments (including controls) were assigned initially to individual plots at random. Each plot had a 1·5-m wide fireline ploughed around its perimeter, and no sampling was conducted within a 5-m zone from the plot edge. Our research focused on the 2-year interval plots because previous fire history research has shown the natural (pre-Euro-American settlement) fire-return interval to be approximately every 2 years in this area (Dieterich 1980). More site characteristics including information on burning conditions can be found in Covington & Sackett (1986) and Wright & Hart (1997).

Soils in the Chimney Spring area are derived from late Tertiary flow basalt and are classified as Brolliar stony clay loam, a fine, smectitic, frigid Typic Argiboroll. The overstorey consists of uneven-aged ponderosa pine in small, approximately even-aged groups (Covington & Sackett 1986). Understorey density was very low within the study area (Harris & Covington 1983; see below).

SOIL SAMPLING

We sampled mineral soil (0–15 cm) from three replicate plots in each of the 2-year interval burn and control treatments. The majority of tree fine roots occur within this soil layer in these forests (Wright & Hart 1997). Sampling spanned the two intervening growing seasons after the 1992 burn to 1 week following the 1994 burn. Prior to the 1994 burn, the 2-year interval plots had been repeatedly burned eight times following the initial burn in 1976. There was no manipulation of the forest floor (O horizon) or fuel loads prior to burning. We sampled soils in each 1-ha plot within three different ponderosa pine canopy substands, which were delineated based upon the dominant tree diameter (Covington & Sackett 1986, 1992): a yellow pine substand containing trees > 28 cm in diameter at breast height (*c.* 1·4 m, d.b.h.; 200–500 years old); a pole substand containing trees 10–28 d.b.h. (80–120 years old); and a sapling substand containing trees 0–10 cm d.b.h. (60–70 years old). We used this stratified sampling design because previous research at this site indicated that the response of the forest floor and soil characteristics to prescribed burning strongly depended on substand classification (for details see Wright & Hart 1997). Grass openings between pine substands were not

sampled because they represented only a few per cent of the area in each plot (Covington & Sackett 1992).

One substand of each type was randomly selected within each plot. Four intact soil cores (4·8 cm inner diameter; AMS Core Sampler, American Falls, ID) were taken from a randomly designated 36-m² sampling area within each substand in each of the six plots. One of these cores was used in part of a companion study that evaluated changes in nitrogen (N) and phosphorus (P) status following repeated burning (Wright & Hart 1997). Sampling was conducted on a monthly basis (about mid-month) during the growing seasons of 1993 (May–November) and 1994 (April–October). Intact soil cores were placed in polyethylene bags and kept in a cooler on ice for transport back to the laboratory; soils were stored (a maximum of 4 weeks) at 4 °C.

FINE ROOT AND MYCORRHIZAL ANALYSIS

Fine roots (≤ 2 mm diameter) and mycorrhizae were separated from soil cores using a hydropneumatic elutriator (Scienceware, Pequannock, NJ) and stacked 2-mm and 500-μm sieves (Bledsoe *et al*. 1999). In a shallow pan containing deionized water, root tips that were clearly ectomycorrhizal were then separated from putatively 'non-mycorrhizal' root tips and segments by hand with the aid of a stereoscope. Ectomycorrhizal root tips were identified by the lack of root hairs, bifurcated root tips and the presence of a fungal mantle (Peterson, Massicotte & Melville 2004; Agerer 1987–99). A subset of these samples was observed under a compound microscope to confirm the presence of a Hartig net (Agerer 1987–99). Hereafter, mycorrhizal root biomass (MRB) refers to these mycorrhizal root tips that consist of both host (ponderosa pine) and fungal (mycobiont) tissue (including fungal mantle, external hyphae and rhizomorphs, and Hartig net; *sensu* Langley & Hungate 2003). Harley (1971) reports that about 40% of the dry weight of mycorrhizae is fungal tissue.

It is possible that some of the non-mycorrhizal root tips were infected with ectendomycorrhizal fungi that are frequently found on *Pinus* spp. roots in disturbed sites (Peterson, Massicotte & Melville 2004; Smith *et al*. 2004). These mycorrhizae typically have thin mantles that may not be apparent at low magnification, and in early stages of colonization roots may be monopodial. However, the substantially higher N and P concentrations of MRB than non-MRB (hereafter called fine root biomass or FRB; see below) and the similarity of our values for these groups to previous studies (Langley & Hungate 2003) suggest that inclusion of ectendomycorrhizal root tips in the FRB category was rare.

In 1993, live and dead fine roots were not separated. However, in 1994, live and dead roots were differentiated using visual characteristics and structural criteria (Kaye *et al*. in press). Fine roots were video-digitized using an Agvision computer-imaging root and leaf analysis system to determine overall root length (Decagon Devices Inc., Pullman, WA); the morphology of the mycorrhizal roots (i.e. bifurcated short roots) did not allow length analysis. Compared with root biomass, root length is considered a more direct estimate of the nutrient and water uptake functions of fine roots (Nye & Tinker 1977). After root length measurements, roots were oven-dried at 70 °C for 48 h. Subsamples were ashed at 550 °C in a muffle furnace for 6 h so that all data could be reported on an ash-free, oven-dry weight basis. Biomass values from the three cores taken per substand per month (subsamples) were averaged for biomass and production calculations (see below).

Annual net fine root production was estimated using two different calculations that were both based on sequential coring data scaled to the plot level: (i) by subtracting annual minimum live FRB plus MRB from maximum biomass values; and (ii) by subtracting annual minimum total (live + dead) FRB plus MRB from maximum biomass values (Kaye *et al*. in press). Because we did not sort live and dead pine roots during 1993, annual net fine root production estimates could only be calculated using the second method for this year. These calculations assume implicitly that no net production occurs during the non-growing season (i.e. approximately December–March). Changes in MRB (all considered 'live' based on appearance) were included in these calculations because mycorrhizae are an inseparable extension of the root system (Fogel & Hunt 1983; Langley & Hungate 2003). Furthermore, because of the very low density of understorey vegetation in both the 2-year burn interval and control plots, we rarely encountered roots that were not from ponderosa pine. Hence, the few herbaceous and shrub roots that we did encounter (estimated as < 1% of the total FRB) were excluded from our study.

FINE ROOT DECOMPOSITION

Fine root decomposition was estimated using the buried litter bag technique (Gholz *et al*. 2000). Live fine roots were collected from unburned plots at Chimney Springs within all three substand types in April 2004 (using the procedures described above), rinsed with deionized water, composited into one sample, and then air-dried. Approximately 0·22 g of air-dry, live fine roots were put into 20 × 20-cm DACRON (Bainbridge International Inc., Huntington Beach, CA, USA) cloth bags (55-μm mesh opening), which were then inserted vertically in the mineral soil to a depth of 20 cm. Three bags per substand per plot (total of 54 bags) were placed in the field on 20 June 1994 and were retrieved on 21 November 1994 (154-day incubation). Incubated root samples were air-dried and weighed. Subsamples from the initial live roots (analytical replication of 10) and all incubated fine roots were analysed for water and ash concentration (as described above) and total Kjeldahl N and P concentrations (see below). Mass loss (i.e. decomposition) over the June–November

period was determined by subtracting the incubated, ash-free, oven-dry mass from the original ash-free, oven-dry mass value for each litter bag. A daily decomposition rate constant (k day^{-1}) was also calculated for each bag assuming that mass loss fit a single exponential decay model (Olson 1963). Changes in N and P content of these roots following incubation were calculated from N and P concentrations and fine root mass.

CHEMICAL ANALYSES AND SOIL MICROCLIMATE

Fine root and MRB subsamples from each soil core were finely ground (< 425 μm) and digested using a modified micro-Kjeldahl procedure (Kaye *et al.* in press). Digested samples were analysed for N and P concentrations by flow-injection colorimetry using the salicylate and molybdate-ascorbic acid methods, respectively (QuikChem AE; Lachat Instruments, Milwaukee, WI). Total N and P values for fine roots in 1993 were based on total fine roots (live and dead roots combined). The total N and P values from 1994 were based on live fine roots only. All nutrient concentrations for fine and mycorrhizal roots were expressed on an ash-free, oven-dry mass basis.

Soil water content was monitored monthly within each substand throughout both the 1993 and 1994 growing seasons. Soil water content was determined gravimetrically (water mass loss at 105 °C for 48 h) on mineral soil (0–15 cm) subsamples of the fourth soil core taken from each substand (Wright & Hart 1997). In 1993, soil temperature (7·5-cm mineral soil depth; near midday) was measured monthly within each substand with soil thermometers. In 1994, we used thermisters attached to dataloggers (CR10; Campbell Scientific Inc., Logan, UT) to monitor soil temperature (7·5-cm depth) continuously in each substand of two plots of each treatment. Values taken every minute were averaged to provide daily means.

STATISTICAL ANALYSES

For each year separately, we used two-way repeated-measures analyses of variance (RM ANOVAs) to test the significance of each of two main effects (treatment and substand) on the following response variables: fine root length density; FRB, N concentration and content, and P concentration and content; and MRB, N concentration and content, and P concentration and content. For the decomposition study, two-way ANOVAs were used to determine significant effects of treatment and substand on mass loss, the decomposition rate constant, and N and P content of the remaining root litter. Plot-level responses ($n = 3$ for both treatments) to treatment were evaluated by scaling substand values using the areal representation of substands within each plot; these plot-level values were then analysed by one-way RM ANOVAs on these same response variables. Similarly, one-way ANOVAs were used to evaluate plot-

level effects of treatment on the fine root decomposition variables noted above. The Holm-Sidak method was used to compare means when ANOVAs were statistically significant. *T*-tests were used to compare fine root net production estimates between treatments and to evaluate whether these estimates were significantly different from zero. Pearson correlation coefficients were used to test for temporal covariance among fine root and mycorrhizal root variables. Data were log$_{10}$-transformed when necessary to meet the normality and homoscedasticity criteria for ANOVAs; however, values presented here are means and standard errors of raw (i.e. untransformed) data. The alpha (*P*) value to denote statistical significance for all statistical analyses was set at 0·05. All statistical analyses were performed using SigmaStat software (V. 3·0; Systat Software, Pt. Richmond, CA).

Results

FINE ROOT AND MYCORRHIZAL ROOT DYNAMICS

Averaged over the 1993 and 1994 growing seasons, total (live + dead) fine root length densities (FRLD) were 28% and 26% lower, respectively, in burned plots than in control plots ($F = 58·02$, $P < 0·001$, $n = 21$ for 1993, and $F = 56·03$, $P < 0·001$, $n = 21$ for 1994; Fig. 1). In 1994, when live and dead roots were separated, FRLD of the live component was 31% lower in the burned plots than in the control plots; FRLD of dead roots was similar between the two treatments and accounted for less than 30% of the total FRLD in both treatments (Fig. 1). Live, dead and total FRLD differed among substands in both treatments (no significant treatment–substand interactions), with significantly higher values in the sapling and pole substands compared with the yellow pine substands for live and total FRLD; yellow pine substands had significantly higher
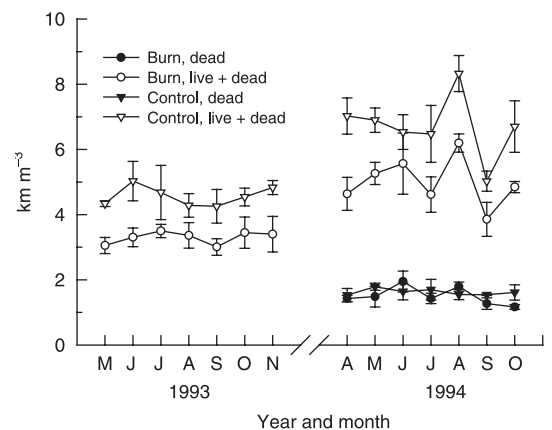

Fig. 1. Fine root length density in burned and control plots during the 1993 and 1994 growing seasons. In 1993, live and dead roots were not separated. Vertical bars represent ± one SEM (*n* = 3). Treatment (burned vs. control) had a statistically significant effect (*P* < 0·05) on all measured fine root length density components except for dead roots in 1994.

Table 1. Mean FRLD, FRB and MRB in different substands during the 1993 and 1994 growing seasons

Below-ground component	1993			1994		
	Sapling	Pole	Yellow pine	Sapling	Pole	Yellow pine
FRLD (km m^{-3})						
Live	ND	ND	ND	4·73^b	4·55^b	3·43^a
Dead	ND	ND	ND	1·45^a	1·44^a	1·94^b
Live + dead	4·26^b	3·99^b	3·52^a	6·17^b	5·98^b	5·37^a
FRB (g m^{-2})						
Live	ND	ND	ND	220^b	238^b	170^a
Dead	ND	ND	ND	54·9^a	52·6^a	78·6^b
Live + dead	287^b	269^{ab}	244^a	275^{ab}	291^b	249^a
MRB (g m^{-2})	46·7^b	35·8^a	33·9^a	52·4^a	47·1^a	45·8^a

In all cases, data were pooled between treatments (burned and control) because there were no significant treatment–substand interactions. Within a given year, substand values for a given below-ground component that have different superscript letters are significantly different ($P < 0.05$). ND, no data.
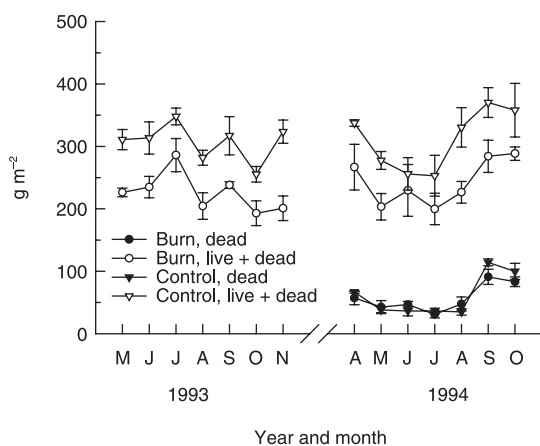

Fig. 2. FRB in burned and control plots during the 1993 and 1994 growing seasons. In 1993, live and dead roots were not separated. Vertical bars represent ± one SEM ($n = 3$). Treatment had a statistically significant effect ($P < 0.05$) on all measured FRB components except for dead roots in 1994.
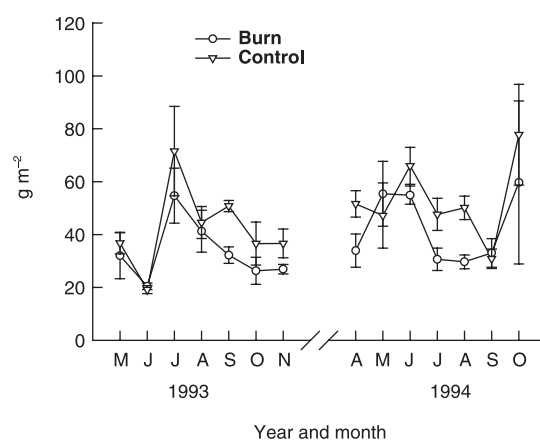

Fig. 3. MRB in burned and control plots during the 1993 and 1994 growing seasons. Vertical bars represent ± one standard error of the mean ($n = 3$). Treatment had a statistically significant effect ($P < 0.05$) on MRB in 1993 but not in 1994.

FRLD of dead roots than the other substands (Table 1).

Differences in FRB pools between treatments were similar to differences in FRLD. Averaged over the 1993 and 1994 growing seasons, total FRB was 26% and 22% lower, respectively, in burned plots than in control plots ($F = 84.79$, $P < 0.001$, $n = 21$ for 1993, and $F = 33.16$, $P < 0.001$, $n = 21$ for 1994; Fig. 2). Total FRB and total FRLD were correlated in both years ($r = 0.774$, $P < 0.001$, $n = 42$, and $r = 0.479$, $P = 0.001$, $n = 42$, for 1993 and 1994, respectively); this correlation appeared to be driven by live roots because live FRB and live FRLD were also correlated in 1994 ($r = 0.749$, $P < 0.001$, $n = 42$) but dead FRB and dead FRLD were not (Figs 1 and 2). FRB and FRLD components also showed similar patterns among substands (Table 1).

In 1993, MRB was about 21% lower in burned plots than in control plots ($F = 6.50$, $P = 0.019$, $n = 21$) but there was no significant difference in MRB between treatments in 1994 ($F = 2.19$, $P = 0.155$, $n = 21$; Fig. 3). MRB tended to be higher in sapling substands than in

pole and yellow pine substands; however, this difference was only significant in 1993 (Table 1). Temporal changes in MRB did not consistently follow changes in FRB components (Figs 2 and 3). In 1993, MRB was weakly correlated with total (live + dead) FRB ($r = 0.394$, $P = 0.010$, $n = 42$) but MRB was uncorrelated with any root component (live, dead or total) in 1994. Additionally, MRB values were only 13–18% the magnitude of the corresponding total FRB pools across treatments and years.

FINE ROOT PRODUCTION AND DECOMPOSITION

In the maximum–minimum method where only live fine roots (including mycorrhizal roots) were considered, net fine root production in 1994 was estimated to be 114 ± 30 g m^{-2} year^{-1} in the burned plots and 115 ± 11 g m^{-2} year^{-1} in the control plots. Only the net production estimate for the control plots was statistically significant from zero. When changes in total FRB

Table 2. Mean N and P concentrations in FRB and MRB in different substands during the 1993 and 1994 growing seasons

Below-ground component	1993			1994		
	Sapling	Pole	Yellow pine	Sapling	Pole	Yellow pine
N concentration						
FRB (g N kg^{-1})						
Live	ND	ND	ND	5·59	4·99	6·27
Dead	ND	ND	ND	ND	ND	ND
Live + dead	6·24	6·47	7·27	ND	ND	ND
MRB (g N kg^{-1})	13·9[a]	14·3[a]	16·3[b]	16·0[b]	14·9[a]	17·2[c]
P concentration						
FRB (g P kg^{-1})						
Live	ND	ND	ND	0·94[a]	0·92[a]	0·97[a]
Dead	ND	ND	ND	ND	ND	ND
Live + dead	0·88	0·90	0·93	ND	ND	ND
MRB (g P kg^{-1})	1·91[a]	1·76[a]	2·10[a]	2·08[a]	2·10[a]	2·30[a]

In all cases, data were pooled between treatments (burned and control). However, significant treatment interaction with substand occurred for N and P concentrations of live + dead FRB in 1993, and N concentration of live FRB in 1994; statistical tests are not shown for these components. Within a given year, substand values for a given below-ground component that have different superscript letters are significantly different ($P < 0.05$). ND, no data.

and MRB were used in the maximum–minimum calculation, mean net fine root production in 1994 was calculated to be 161 ± 48 g m^{-2} year^{-1} in the burn plots and 169 ± 19 g m^{-2} year^{-1} in the control plots. Again, only the mean value from the control plots differed significantly from zero. Using this method to calculate net fine root production in 1993 (where live and dead roots were not separated), we estimated the mean value for the burn plots to be 130 ± 14 g m^{-2} year^{-1} in the burn plots and 138 ± 8 g m^{-2} year^{-1} in the control plots. In this case, both estimates differed significantly from zero. Regardless of calculation method or year, no statistically significant difference in net fine root production between treatments was found.

Similar to net fine root production estimates, we found no statistically significant difference in root decomposition rates or nutrient dynamics between treatments. Mean mass loss from fine roots over the 154-day period in the burned plots was $24·4 \pm 5·6\%$ and in control plots $16·8 \pm 1·9\%$. The calculated daily decomposition constant was $0·0020 \pm 0·0005$ day^{-1} in the burned and $0·0012 \pm 0·0001$ day^{-1} in the control plots. The mean percentage of the original N mass remaining after the 154-day period was $78·9 \pm 3·9\%$ and $85·0 \pm 5·1\%$ for the burned and control plots, respectively. Similarly, the mean percentage of the original P mass remaining in the roots was $9·0 \pm 0·4\%$ and $9·4 \pm 0·8\%$ for the burned and control plots, respectively. The substand where the root litter decomposed was not a significant factor for any of these decomposition variables, nor were there any significant interactions between treatment and substand.

NITROGEN AND PHOSPHORUS CONCENTRATIONS AND CONTENTS

Total N and P concentrations (g kg^{-1}) in total (live + dead) fine roots in 1993 differed significantly by treatment and substand; significant interactions between treatment and substand also occurred (Table 2). In 1994, when only live roots were analysed for their nutrient concentration, treatment and substand (and treatment–substand interaction for N concentration) were all significant factors affecting root nutrient concentrations (Table 2).

Total N concentration in mycorrhizal roots in 1993 and 1994 was not influenced by treatment but was significantly different among substands and no interaction between these factors occurred (Table 2). Total P in mycorrhizal roots was not affected significantly by treatment or substand in 1993 or 1994 (Table 2). Total N and P concentrations in mycorrhizal roots were about 2·9 and 2·3 times higher, respectively, than in live fine roots in 1994 (Table 2).

Total fine root N and P contents (g m^{-2}) in 1993 were 31% and 36% lower, respectively, in burned plots than control plots ($F = 197·68$, $P < 0·001$, $n = 21$ for N, and $F = 248·22$, $P < 0·001$, $n = 21$ for P; Fig. 4). Similarly, in 1994 when only live fine roots were analysed, fine root N and P contents were 31% and 27% lower, respectively, in burned plots than in control plots ($F = 23·47$, $P < 0·001$, $n = 21$ for N and $F = 17·55$, $P < 0·001$, $n = 21$ for P; Fig. 4). Total N and P contents in mycorrhizal roots were 23 and 27% lower, respectively, in burned plots than control plots in 1993 ($F = 5·10$, $P = 0·035$, $n = 21$ for N, and $F = 7·57$, $P = 0·012$, $n = 21$ for P), while only total N was significantly lower (30%) in 1994 ($F = 7·30$, $P = 0·014$, $n = 21$; Fig. 4).

SOIL MICROCLIMATE

Soil temperature (7·5 cm mineral soil depth) was significantly higher in the burned plots than the control plots in both years (Fig. 5). In 1993, burned plots were on average 2·2 °C warmer, while in 1994 they were on average 1·6 °C warmer. In contrast, soil water content
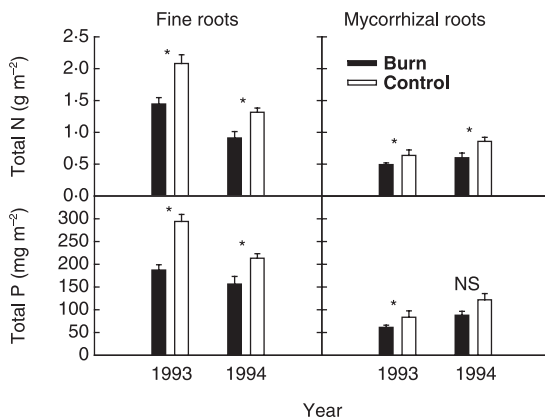
Fig. 4. Mean N and P content in fine and MRB in burned and control plots in 1993 and 1994. In 1993 fine root values included both live and dead roots, while in 1994 values included only live roots. Vertical bars represent + one SEM (n = 3). An asterisk denotes that the treatment had a statistically significant effect on that nutrient component (P < 0·05). NS, not significant.
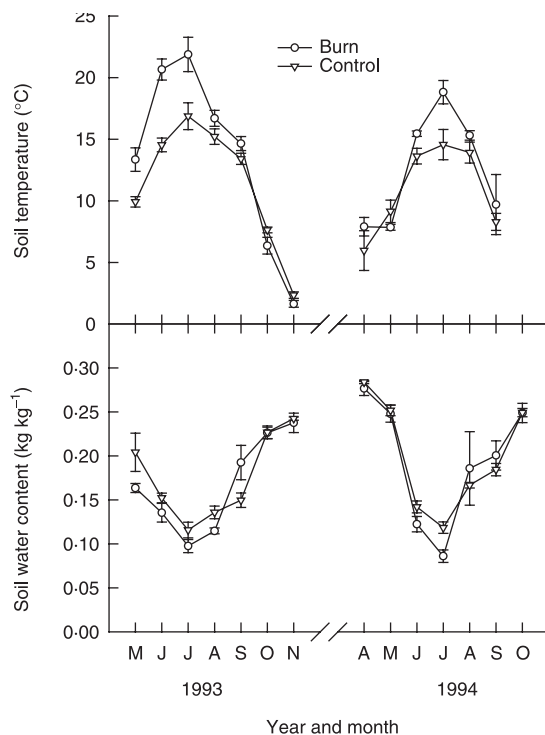

Fig. 5. Mean soil temperature (7·5-cm mineral soil depth) and soil water content (0–15-cm depth) in burned and control plots during the 1993 and 1994 growing seasons. In 1993, soil temperature values represented temperatures taken near midday using soil thermometers, while 1994 values represented daily averages measured using dataloggers and thermocouples. Vertical bars denote ± one SEM (n = 3 in 1993 and n = 2 in 1994). Treatment had a statistically significant effect (P < 0·05) on soil temperature in both years; however, soil water content was statistically similar between treatments in both years.

(F = 4·03, P = 0·025, n = 21 for 1993 and F = 6·20, P = 0·005, n = 21 for 1994). Sapling substands generally had higher soil water contents than the other substands.

Discussion

Few studies have assessed below-ground biomass pools and nutrient cycling processes in forests of the south-western USA (Wright & Hart 1997; Kaye & Hart 1998a, b; Korb, Johnson & Covington 2003; Haskins & Gehring 2004; Kaye *et al.* in press). Although there have been a few investigations of the effects of a single burn on fine roots and mycorrhizae in pine-dominated forests that evolutionarily experienced frequent fire (Korb, Johnson & Covington 2003; Haskins & Gehring 2004; Smith *et al.* 2004), we know of no other study that has evaluated the effects of repeated-prescribed burns on the biomasses of these key ecosystem components in any forest (but see Tuininga & Dighton 2004 for repeated-prescribed fire effects on ectomycorrhizal diversity).

We found that repeated-prescribed burns at Chimney Spring significantly reduced FRLD (26–28%), total FRB (22–26%) and MRB (21% in 1993 only). These results are consistent with previous work that found both low- and high-intensity burns in ponderosa pine forests significantly reduced fine roots (Grier 1989; Swezy & Agee 1991; Stendell, Horton & Bruns 1999), and that burning (prescribed and wildfire) in many ecosystems negatively impacts mycorrhizal mutualists (Parke, Linderman & Trappe 1983; Stendell, Horton & Bruns 1999; Haskins & Gehring 2004; Hart *et al.* in press).

Changes in the vegetation structure caused by the repeated burnings may, in part, be responsible for these changes in below-ground components. Although stand basal area was unaffected by repeated burnings, stem density in burned plots was reduced by 38% compared with the unburned control plots (last measured in 1988 after six burns by Peterson *et al.* 1994). Repeated interval burning resulted in the conversion of sapling substands to pole and, to a lesser degree, yellow pine substands (S.S. Sackett, unpublished data), and sapling substands tended to have higher FRB and MRB values than the other substands (Table 1). Kaye & Hart (1998b) also found lower total FRB in ponderosa pine substands that had lower tree densities. However, we found no significant treatment–substand interaction for any below-ground biomass pool in either year; this result suggests that burning consistently reduced these below-ground components regardless of substand. Hence, we conclude that repeated-prescribed burning has fundamentally altered the relationship between above- and below-ground biomass pools. Changes in above-ground-to-below-ground allometry may have occurred from direct mortality of fine and mycorrhizal roots from repeated fire (Hart *et al.* in press), as well as from reduced carbon allocation below-ground in burned compared with control plots in response to reduced tree vigour following burning (Peterson *et al.* 1994).

(0–15 mineral soil depth) was similar between treatments in both years (Fig. 5). Substand did not significantly affect soil temperature, but soil water content was affected significantly by substand in both years

We speculate that these changes in below-ground components occurred during the first few prescribed burns, when fuel loads and thus fire intensities were highest (Covington & Sackett 1992; Peterson *et al*. 1994). We base this hypothesis on the result that these biomass pools did not seem to respond immediately to the direct effects of a repeated fire, as indicated by a similar pattern among these pools between burned and control treatments in the sampling dates immediately before and 1 week following the October 1994 burn (Figs 1–3).

Several studies have found decreased carbon allocation to ectomycorrhizae and decreased FRB and root production in response to increased soil N availability. This pattern is generally explained by the apparent decreased 'need' for these soil resource-acquiring structures with greater soil resource availability (Barnes *et al*. 1998; Treseder *et al*. 2004). We have previously reported that soil total N and N availability were lower in the 2-year interval burned plots than in control plots (Wright & Hart 1997). Hence, the reductions in FRB and MRB observed in the burned plots suggest that changes in N availability are probably not responsible for the changes in FRB and MRB observed in these ponderosa pine forests.

Repeated-prescribed fire appeared not to impact the relative degree of mycorrhizal abundance in this ponderosa pine forest in that MRB and FRB were reduced in burned plots to a similar degree. Few studies have measured the amount of MRB in forests. Using methods similar to those in our study, Fogel & Hunt (1983) measured FRB (5-mm diameter) and MRB over a 2-year period in a young Douglas fir *Pseudotsuga menziesii* (Mirb.) Franco forest in the Pacific North-West and found that MRB was 400–800% greater than total FRB. We found that MRB was only 14–17% of the total FRB (2-mm diameter) in the ponderosa pine forests studied, and this proportion was not affected by burning or year. In a Norway spruce stand *Picea abies* (L.) Karst. using a combination of root trenching and biochemical markers (ergosterol and phospholipid fatty acids), Wallander *et al*. (2001) estimated that ectomycorrhizal external mycelia and mantles were between 70 and 90 g m^{-2} in the humus layer; this amount was approximately 1/3 of the FRB in this forest in south-western Sweden. Using a combination of tree girdling and chloroform-fumigation extraction in a Scots pine *Pinus sylvestris* L. stand in northern Sweden, Högberg & Högberg (2002) estimated that ectomycorrhizal mycelia was about 14·5 g m^{-2} in the organic horizon (F + H). The ectomycorrhizal biomass values from these latter two studies in boreal forests are within the range of values found for MRB in the upper mineral soil of the ponderosa pine forests we studied, especially considering we measured very little external mycelia. Differences among forests could be the result of a variety of factors, including differences in climate, measurement technique, horizon(s) sampled and mycobiont–host relationships (Read *et al*. 1992).

Although FRLD, FRB and MRB were higher in burned than control plots, estimates of net fine root production and root decomposition rates were generally similar between treatments. Maximum–minimum estimates of fine root production across treatments, years and method of calculation (i.e. whether dead roots were included or not) ranged between 114 g m^{-2} year^{-1} and 169 g m^{-2} year^{-1}. These values are lower than those found by Kaye *et al*. in press) at the Gus Pearson Natural Area (GPNA) over the same sampling depth and using similar methods; at GPNA, net pine fine root production was estimated at about 210 g m^{-2} year^{-1}. The fine root production values at Chimney Spring were 36–54% the magnitude of annual litterfall (< 10-cm diameter) in the control plots (Covington & Sackett 1990).

We found no significant difference between treatments in root decomposition rate or nutrient dynamics of roots during decomposition despite warmer soil temperatures and lower N availability (Wright & Hart 1997) in the burned plots. It is possible that the generally positive effect of warmer soil temperatures on decomposition processes were negated by the generally negative effect of lower soil N availability, resulting in similar decomposition dynamics between the treatments (Paul & Clark 1996). The overriding effect of soil water content, which was similar between treatments, on decomposition processes in ponderosa pine forests may also have obscured these other factors (Hart, Firestone & Paul 1992). We know of no other studies that have evaluated root decomposition rates in ponderosa pine forests of the south-western USA, but our estimates of root decomposition are similar in magnitude as those observed for slash pine *Pinus elliottii* Engelmann fine roots decomposing across a wide range of temperate forests (Gholz *et al*. 2000). Our estimates of ponderosa pine root decomposition rates were higher than those found for ponderosa pine needle litter decomposing on the surface of the forest floor in these south-western USA ecosystems (Klemmedson, Meier & Campbell 1985; Hart *et al*. in press). Furthermore, decomposing roots released substantially more N and P in their first year of decomposition than needle litter decomposing in a nearby ponderosa pine forest (Hart *et al*. in press). We do not know if N and P will continue to be released from ponderosa pine roots after one growing season of decomposition, but if this trend is maintained over time then nutrient turnover in fine roots may be a major source of available nutrients in these forests (Hart *et al*. in press).

Even though MRB was only 21–23% of the live FRB in 1994, the substantially higher nutrient concentrations in mycorrhizal roots resulted in these tissues containing about 70% and 60% as much N and P, respectively, as live fine roots. Although these stocks are substantial, Fogel & Hunt (1983) reported that mycorrhizal roots contained 490% and 620% the amount of N and P, respectively, as fine roots. Because N and P concentrations of MRB in the Douglas fir forest were lower than ours (6·23 g N kg^{-1} and 1·48 g P

kg^{-1}) while nutrient concentrations in fine roots were similar, these differences between forests are driven by the substantially greater amount of MRB in the Douglas fir forest, or perhaps differences in the efficiencies by which these below-ground components were extracted from the soil in the two studies. The amount of N stored in MRB in repeatedly burned and control plots in the ponderosa pine forest in our study is similar in magnitude to the amount of N contained in ectomycorrhizal mycelia in a Norway spruce forest in south-western Sweden (estimated to be about 0·38 g N m^{-2}; Nilsson & Wallander 2003).

These results support our previous conclusions (Wright & Hart 1997) that although a 2-year interval burn cycle may be effective for reducing and then maintaining fuel loads in south-western ponderosa pine forests, prescribed burning at this frequency may have deleterious effects on ecosystem function. Although we could not detect any change in below-ground productivity as a result of this treatment regime, our results are consistent with the speculation made by Peterson *et al*. (1994) that the reduced above-ground productivity in burned plots is likely to be a result of a sustained reduction in FRB and MRB, as well as a decline in N availability (Wright & Hart 1997). Such negative effects from re-establishing a natural frequent fire regime in these forests may be avoided by mechanically removing some of the accumulated fuel prior to prescribed burning (Covington *et al*. 1997). Short-term results from the ecological restoration study at the nearby GPNA support this conclusion, as no change in above- or below-ground production was observed when restoration activities included manual removal of accumulated fuels prior to the reintroduction of fire (Kaye *et al*. in press).

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